Shared networks for auditory and motor processing in professional pianists: Evidence from fMRI conjunction

Marc Bangert,[a,b,c,*] Thomas Peschel,[c,d] Gottfried Schlaug,[b] Michael Rotte,[d] Dieter Drescher,[a] Hermann Hinrichs,[d] Hans-Jochen Heinze,[d] and Eckart Altenmüller[a,*]

[a]Institute of Music Physiology and Musicians' Medicine, Hanover University of Music and Drama, Hohenzollernstrasse 47, D-30161 Hanover, Germany
[b]Department of Neurology, Beth Israel Deaconess Medical Center and Harvard Medical School, 330 Brookline Ave., Boston, MA 02215, USA
[c]Klinik für Neurologie, Medizinische Hochschule Hannover, Carl-Neuberg-Str. 1, D-30625 Hanover, Germany
[d]Klinik für Neurologie II, Otto von Guericke Universität, Magdeburg, Germany

To investigate cortical auditory and motor coupling in professional musicians, we compared the functional magnetic resonance imaging (fMRI) activity of seven pianists to seven non-musicians utilizing a passive task paradigm established in a previous learning study. The tasks involved either passively listening to short piano melodies or pressing keys on a mute MRI-compliant piano keyboard. Both groups were matched with respect to age and gender, and did not exhibit any overt performance differences in the keypressing task. The professional pianists showed increased activity compared to the non-musicians in a distributed cortical network during both the acoustic and the mute motion-related task. A conjunction analysis revealed a distinct musicianship-specific network being co-activated during either task type, indicating areas involved in auditory-sensorimotor integration. This network is comprised of dorsolateral and inferior frontal cortex (including Broca's area), the superior temporal gyrus (Wernicke's area), the supramarginal gyrus, and supplementary motor and premotor areas.

Introduction

Over the past years, musicians have gained ever-increasing attention within the field of brain research in general, and neuroimaging in particular. The reasons for this are two-fold: first, musicianship provides an excellent model for deliberate long-term practice and thus for brain plasticity in both structural and functional respects. Changes due to the training of instrumental motor skills can occur very rapidly (Pascual-Leone et al., 1995; Bangert and Altenmüller, 2003; Stewart et al., 2003); lifelong practice might even alter macrostructural anatomy (Schlaug et al., 1995; Elbert et al., 1995; Gaser and Gottfried Schlaug, 2003). Secondly, since the mastering of a musical instrument requires some of the most sophisticated skills, including fast and interlaced auditory, visual, and motor processing, music performance offers answers to a variety of questions concerning multisensory as well as sensorimotor integration. While other research has addressed visuomotor integration of notated music (Stewart et al., 2003), the present article focuses on audiomotor integration. The instrument transforms the highly trained movement patterns into successions of acoustic events. Therefore, any self-monitoring during musical performance has to rely on quick feedforward and feedback models that link the audible targets to the respective motor programs.

It seems likely then that auditory and motor networks are strongly linked in the musician's brain, and that even when the task involves only auditory or only motor processing, co-activation phenomena within the respective brain areas can be expected: Haueisen and Knösche (2001) showed that pianists listening to well-trained piano music exhibit covert (unconscious) contralateral primary motor cortical activity. Motor-to-auditory co-activation has been shown by Lotze et al. (2003) with functional magnetic resonance imaging (fMRI) of violinists and amateurs silently tapping out a well-trained concerto. Using fMRI, Meister et al. (2004) compared music performance and music imagery in musicians performing a familiar piece. In both conditions, they found activations of a bilateral frontoparietal network comprising the premotor areas, the precuneus and the medial part of BA 40. During music performance, but not during imagery, the contralateral M1 and bilateral PPC were active. An activation with a clear lateralization in their study was found in the left posterior part of the dorsolateral prefrontal cortex (Meister et al., 2004). Similar co-activation phenomena are known from the speech literature, where the classical notion of a functional

* Corresponding authors. M. Bangert is to be contacted at Department of Neurology, Beth Israel Deaconess Medical Center and Harvard Medical School, 330 Brookline Ave., Boston, MA 02215, USA.
E-mail addresses: bangert@gmx.com (M. Bangert), altenmueller@hmt-hannover.de (E. Altenmüller).
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dissociation of speech perception and speech production has recently been adjusted towards a joint sensorimotor representation (Aboitiz and Garcia, 1997; Watkins and Paus, 2004; Watkins et al., 2003).

The aforementioned musician studies share a general shortcoming of many studies dealing with musical skills: because of the very nature of the tasks (they require the investigated skill, such as instrumental performance of complex movement patterns, ear training, reading notation, etc.), a control group of non-musicians often cannot be introduced. In speech research, it is inherently more problematic to introduce a naïve control group. If a control group is missing, the problem arises to disentangle to what extent the observed brain activation is due to musicianship (plasticity effect) or task inherent (e.g., complexity effect). The use of simple perceptual and motor tasks has been successfully demonstrated by Bangert and Altenmüller (2003) for an EEG paradigm and by Haslinger et al. (2005) for an fMRI paradigm, the latter, however, focusing on visual action observation accompanying auditory stimulation rather than on auditory presentation of piano playing alone.

Therefore, we opted to employ a special set of tasks, which has been originally introduced as the "probe task paradigm" in a previous training study (Bangert and Altenmüller, 2003) for a cross-sectional comparison of a group of professional pianists and a control group of non-musicians. These tasks required either *passive listening* or *silent finger movement* and were therefore either *purely acoustic* or *purely motion-related*. This, of course, relates to the physical setup of the experiment, and not necessarily to the way the task is cognitively processed. The motion-related task, for instance, is non-*acoustic* because no sound is generated, however, it may be *auditory* if the cognitive processes triggered by it include auditory imagery, active or passive. It is important to note that the paradigm aims at automatic processes (tasks are passive) but not pre-attentive processes (no distractor task to divert attention is introduced). The tasks are passive in the sense that the average brain responses are evoked automatically (and reported as such by the subjects) rather than deliberately. A major advantage of using passive tasks is that they are simple enough to be performed by an untrained control group—no particular skill is required. Yet the tasks are specific enough to engage brain areas related to the skill in the skilled group.

Because the two task types dissociate the *external* correlate (piano tones–piano keys) of a putative cognitive auditory-sensorimotor link, the paradigm can be nicely combined with a conjunction approach to analyze the functional MRI data acquired with the tasks. Conjunction analyses can be applied between conditions (Price and Friston, 1997), between sessions, and between subjects (Friston et al., 1999). In this study, we utilized between-conditions conjunction.

Materials and methods

Subjects

Two groups of subjects participated in the study after giving informed consent: eight professional pianists and graduate piano students recruited from the University of Music and Drama Hannover, Germany, and eight students from other Hannover colleges, with no formal instrumental training. The data were obtained in 2003 at the ZENIT Center, Neuroimaging Department, Magdeburg, Germany. After acquisition of the fMRI data, one subject in each

group had to be discarded due to MRI signal artifacts (CSF 'activations'). The final analysis comprised the following groups:

> Pianist group: 7 subjects, 3 male; mean age 28.5 ± 7.3 years, with an accumulated lifetime practice experience of 20.0 ± 8.7 years of practice. Age of commencement of piano training was 8.5 ± 4.8 years.
>
> Non-musician group: 7 subjects, 3 male; mean age 28.4 ± 5.8 years. The control subjects were selected to meet the criterion that they never received any lessons for a musical instrument or attempted to play any musical instrument.

All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were scanned in an fMRI device (details see below) while they performed an 'acoustic task' and a 'motion-related task' in a block design.

Tasks

The acoustic task (aT) required passively listening to 3-s monophonic piano sequences.

The stimuli were real-time synthesized (and therefore randomized) by a computer algorithm taking into account pitch transition probabilities as customary with classical European music. The note range was $c'–g'$; the entire pattern consisted of five quaver (1/4) notes (beats) at tempo 100 beats-per-minute, plus one additional crotchet (1/8) note between two beats at a random position.

Auditory stimuli were D/A converted by a PC Soundcard (SoundBlaster™ compatible) and delivered to the subject using a high-frequency shielded transducer system as described in Jäncke et al. (2002). The transmission system includes a piezoelectric loudspeaker enabling the transmission of strong sound pressure levels (~105 dB) with excellent attenuation characteristics. These loudspeakers are embedded in tightly occlusive headphones allowing unimpeded conduction of the stimulus with suppression of ambient scanner noise by about 20 dB. Additionally, noise-protection ear plugs within the loudspeakers provided an additional noise attenuation of about 15–20 dB, resulting in a total noise attenuation of 35–40 dB (Jäncke et al., 2002).

The melodies were cued and accompanied by the visual presentation of an 'ear' symbol on a small overhead projection screen.

In the motion-related task (mT), subjects were prompted to arbitrarily press keys on a soundless piano keyboard during a time window of 3 s. The piano keyboard we used is a custom designed one-octave part of an actual Acoustic Grand Piano keyboard, being stripped off any ferromagnetic component and tested for MEG and MRI compliance. The action mechanism was kept fully functional to preserve the mechanical 'feel' for pianists. Information about the hammer speed was picked up by dual photoelectric barriers and transferred by means of optical fibers to an electronic processor outside the scanner, where the signal was A/D-converted and translated into a standard serial interface protocol (MIDI), which carries information about key number and hammer velocity. This MIDI information was then used in a PC for real-time control of the experiment, and for offline performance analysis.

Beginning and end of movement time were indicated by a small color-changing 'keyboard' symbol on the screen. The five digits of the right hand rested on the five white keys $c'–g'$, corresponding to the pitch range of the melodies in the acoustic tasks.

Details about the melody algorithm, timing of the stimulus presentation, and timing of the visual cues during the epochs are specified in Bangert and Altenmüller (2003).

Neither task required a specific cognitive involvement; the instruction simply was to attend the fixation symbol while listening or moving. Since no kind of response was required (memorization, decision-making, etc.), no specific cognitive strategy was indicated, and no explicit instruction was given to actively imagine sounds and movement, neither to suppress imagery. The subjects rather were instructed "to relax and not to attend to anything else but the fixation symbol".

Experimental design

A blocked design was used. All volunteers had six fMRI runs of five stimulation/baseline cycles each. Each of the six runs had the following identical structure:

- 4 rest trials (discarded),
- 5 repetitions of the block sequence: [6 acoustic probe trials (aT)−4 rest trials−6 motion-related probe trials (mT)−4 rest trials],
- 4 rest trials (discarded).

A single trial was comprised of 3000 ms stimulus presentation followed by 1500 ms of scan acquisition. In total, 180 aT and 180 mT brain acquisitions were collected from each subject.

Imaging parameters

The imaging was performed on a GE Medical Systems 1.5 T Signa Neurovascular MR scanner with a standard GE quadrature head coil. After positioning of the subject and tight fitting of the head in order to reduce motion, the structural scanning consisted of high resolution T1 weighted SPGR images (60 sagittal slices, 2.8 mm thickness) and anatomic images with identical orientation to the functional echo planar images (23 oblique slices, 5 mm thickness, 1 mm gap). For the functional scanning, images were acquired using single shot gradient echo planar imaging (FOV 20 cm, TR 4.5 s, pass delay 3 s, TE 40 ms) covering the whole head volume. Each run consisted of 108 time points; during each time point, 23 slices (5 mm thickness, skip 1 mm between slices, in plane resolution 3.125 mm) oriented to the plane connecting the anterior and posterior commissure were recorded.

Image processing and statistical analysis were carried out using the SPM99 analysis package (Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB 5.3 software (Mathworks, Natick, MA, USA) on a standard IBM-compatible PC. The first 4 scans were excluded from analysis in order to allow T1 stabilization. Preprocessing of the data took several steps: in the first step, for each functional run, images were realigned to the first image of the session. The resulting mean image of co-registered functional scans of each run was used to determine the individual normalization parameters for each functional session. These images were normalized into a standard stereotactic space using the EPI-template provided by SPM99 resulting in 3-mm isotropic voxels. Finally, images were smoothed using a 9-mm-full-width-at-half-maximum isotropic Gaussian kernel to increase signal to noise ratio and to minimize the effects of individual variations in gyral anatomy (Friston et al., 1995b). These adjusted images were subjected to statistical analysis. Active voxels were searched for using the General Linear Model approach for the time-series data (Friston et al., 1995a). For this, we defined a design matrix comprising contrasts modeling the alternating periods of each task using a boxcar reference vector convolved with a hemodynamic response function. Comparison conditions were defined as two explicit behavioral tasks (aT and mT) and one implicitly modeled rest state. A pilot parameter estimation on the first 2 participating subjects from each group revealed no statistical difference between the resting trials following aT and mT.

Statistical analysis

Both the aTs and the mTs were analyzed separately for the pianist and non-musicians groups.

For each individual subject, the contrasts aT vs. rest and mT vs. rest were estimated in order to assess interindividual variability and consistency of the group contrasts which are described in the following. To address the questions of a musicianship-specific activation during the tasks and of a shared co-activation across the task types, the following group contrasts were predefined and modeled:

Acoustic task: Activation (aT vs. rest) in the pianist group, contrasted to activation (aT vs. rest) in the non-musician group.
Motion-related task: Activation (mT vs. rest) in the pianist group, contrasted to activation (mT vs. rest) in the non-musician group.
Conjunction: A conjunction analysis (Price and Friston, 1997) using an SPM of the minimum t statistic over the two contrasts specified in (a) and (b). This approach preserves only those voxels that are significant (thresholded) in both the contributing SPM maps.

Planned contrasts were performed for the entire sample of subjects in a fixed-effects model. Group differences were computed as paired t tests in order to derive statistical parametric maps (SPMs) of the Z statistic. All SPMs were thresholded at P values below $P < 0.001$ (FWE-corrected) at cluster-level for $T = 5.36$ (aT), $T = 7.6$ (mT with extent threshold 10 voxels), and $T = 5.57$ (conjunction).

Local maxima in the SPMs were correlated to brain anatomy by converting their coordinates from MNI space to Talairach space, and subsequently using the WFU PickAtlas (Maldjian et al., 2003), allowing for a search radius of 9 mm (within the extent threshold of 20 voxels per cluster) for an overlap of gray matter and location of local maxima.

Results

Performance homogeneity

Implications from a putative common activity in the different tasks toward a shared cognitive network can only be made if performance homogeneity is controlled within conditions and across subjects. Three general confounds have to be considered: first, it has to be excluded that activation of motor areas accompanying the aTs generated an actual efferent, i.e., suprathreshold, outflow of motor commands. By monitoring the MIDI information on the key presses, gross finger movements during

the aT can be ruled out. To make sure that even minimal muscle activity did not occur, a simultaneous EMG of the finger muscles of the right hand would have been necessary. This has not been done in the current fMRI study; however, in a previous study (using identical experimental tasks and comparable subject groups) a coregistered EMG showed no deflection during the aT (Bangert and Altenmüller, 2003). In both the previous and the current study, the tasks and the instructions were identical, and the subjects were not aware of or informed about the fact that their finger muscles were monitored by the electrodes placed at the surface of the forearm.

Secondly, it is known that movement rate can have an influence on the magnitude of fMRI activation (Schlaug et al., 1996). Since the mT involved three s of tapping on the keyboard at a self-paced tempo, this possible confound deserved special attention in the analysis of the MIDI data. No statistical differences in the tapping rate between pianists and non-musicians could be found (Fig. 1, left).

Thirdly, histograms of the keyboard hammer velocity were created, as force can have an additional effect on fMRI magnitude in the motor cortex (Dettmers et al., 1995, 1996). Although the professional pianists showed a trend towards higher forces (velocities) when pressing the piano keys (Fig. 1 right), group differences were not significant.

Acoustic task

Passive listening to the piano melodies during the aT activated bilateral primary and secondary auditory cortices in both groups (Figs. 2a, b), including most of the superior temporal gyri (STG) bilaterally. Additional activations were present in the frontal and parietal lobes.

The pianists, however, showed additional activity in frontal, temporal and parietal cortical regions, which are listed in Table 1 and depicted on a surface rendering in Figs. 2b, c. The bilateral group-specific activations were observed in the poste-

rior middle temporal gyri, and in superior frontal gyri and frontal precentral gyri, more specifically primary motor and premotor cortex. Unilateral activation was found in the right superior frontal gyrus (BA 10), and in the left hemisphere in a distributed network comprising frontal paracentral lobule, posterior inferior temporal gyrus, superior temporal gyrus (STG BA 22), and the inferior parietal lobule. On the left hemisphere, a remarkable finding is a strip of activation extending from the primary motor cortex in the precentral gyrus, through premotor frontal areas (BA4/6), to the superior portion of Broca's area (BA 44).

The non-musicians showed group-specific activation (contrasted vs. pianists) mainly in the right posterior STG (Fig. 2d).

Motion-related task

The motion-related task, involving voluntary key presses without auditory feedback on the MRI-compatible grand piano keyboard, activated primary sensorimotor cortex (SM1) bilaterally, postcentral parietal regions, and SMA. This finding was similar in both groups because of the overt movement (Figs. 3a, b).

The group contrast revealed the following additional regions active during the movement (Figs. 3c, d, and Table 1).

Bilaterally, the medial frontal and precentral gyrus, more specifically premotor and supplementary motor area were active in the pianists but not in the non-musicians (Fig. 3c). Furthermore, bilateral dorsolateral prefrontal cortex (dPFC, BA 46) showed greater activation in the pianist group. The BA 46 activation is of special interest here because this is the only region that is activated in the pianists exclusively, i.e., where the activation in the non-musicians is not only weaker, but virtually not present at any statistical threshold.

The right hemisphere displayed group-specific activity in the supramarginal gyrus. Pianist-specific signals lateralized to the left could be observed in the STG (BA22), and in frontal BA44
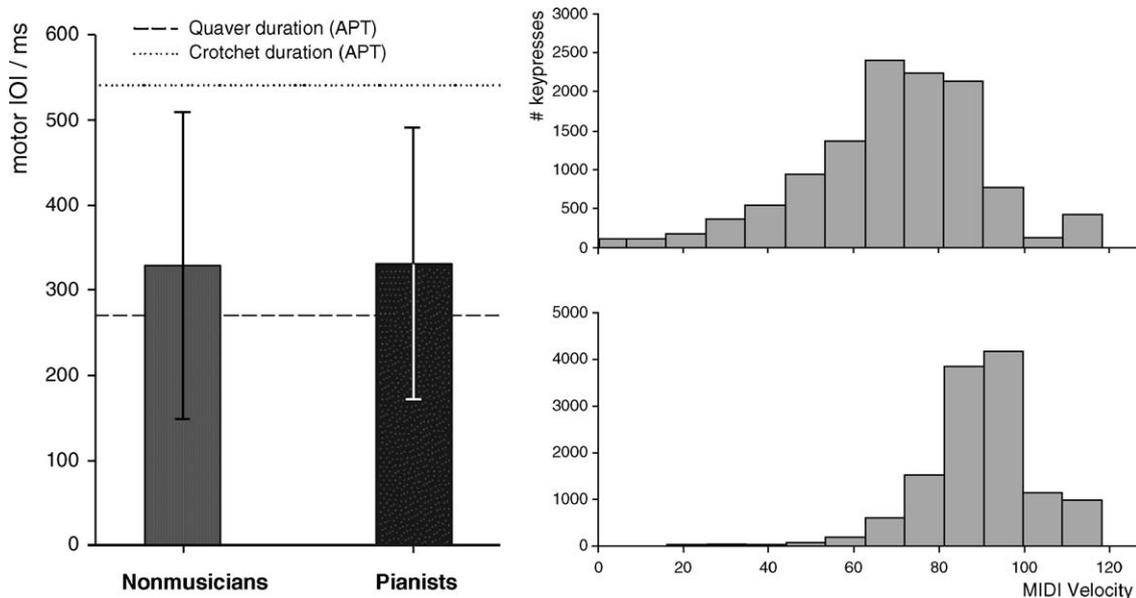

Fig. 1. Performance in the self-paced motion-related task. Left panel: average Inter-Onset-Intervals (error bars = standard deviations) during the mT for the non-musician group (gray) and the pianist group (black). Right panel: histograms of the hammer velocity (the piano keyboard being calibrated and normalized to the MIDI standard with minimum velocity = 1, maximum velocity = 127) of all collected key presses in the mT in the non-musician group (top) and the pianist group (bottom).
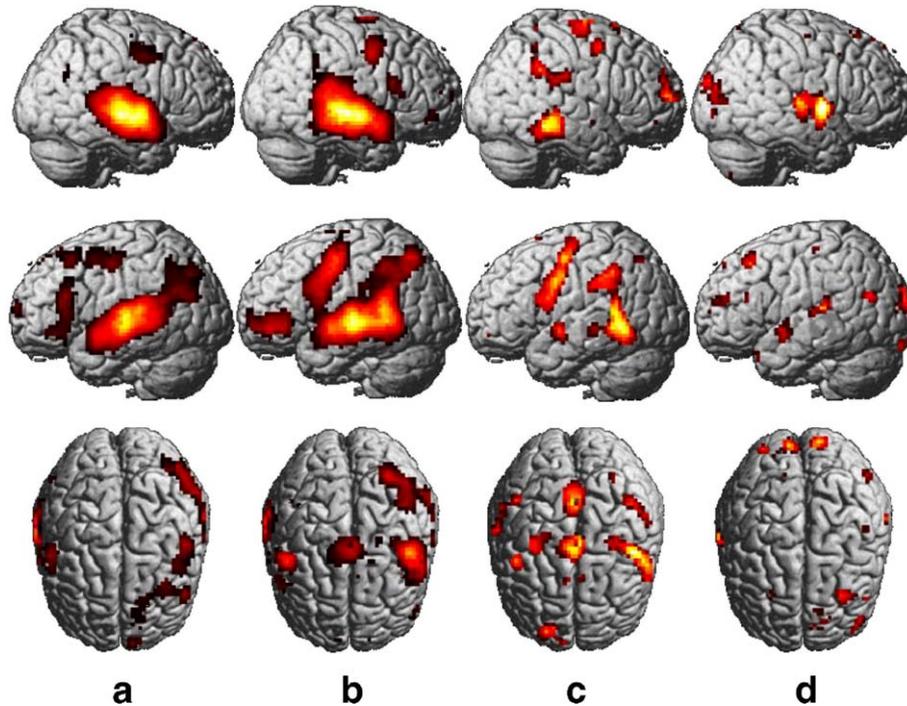
Fig. 2. fMRI group activation during the acoustic task (aT). Different views of a rendering of the SPM maps onto a standard single subject anatomical brain template. (a) Non-musician group (contrasted vs. rest); (b) musician group; (c) activations of the musician group (contrasted vs. non-musicians); (d) activations of the non-musician group (contrasted vs. musicians). SPMs FWE-corrected at cluster-level and thresholded at $P = 0.0001$ (a, b) and $P = 0.005$ (c, d).

(Broca's area). In contrast to the non-musicians' group, the pianists involved additional parts of a limbic network during the motion-related task, including the right hippocampus, right cingulate gyrus and posterior cingulate, and the left parahippocampal gyrus.

The non-musicians showed group-specific activity (Fig. 3d) in the postcentral gyrus bilaterally, the occipital lobe, and the cerebellum.

Auditory-motor conjunction

The conjunction analysis of the two contrasts gained in aT and mT revealed those areas that exhibit a group effect and are active during either task type (Fig. 4 right, and Table 1).

These areas were the middle temporal gyrus bilaterally and the supramarginal gyrus bilaterally. Furthermore, a left frontotemporal
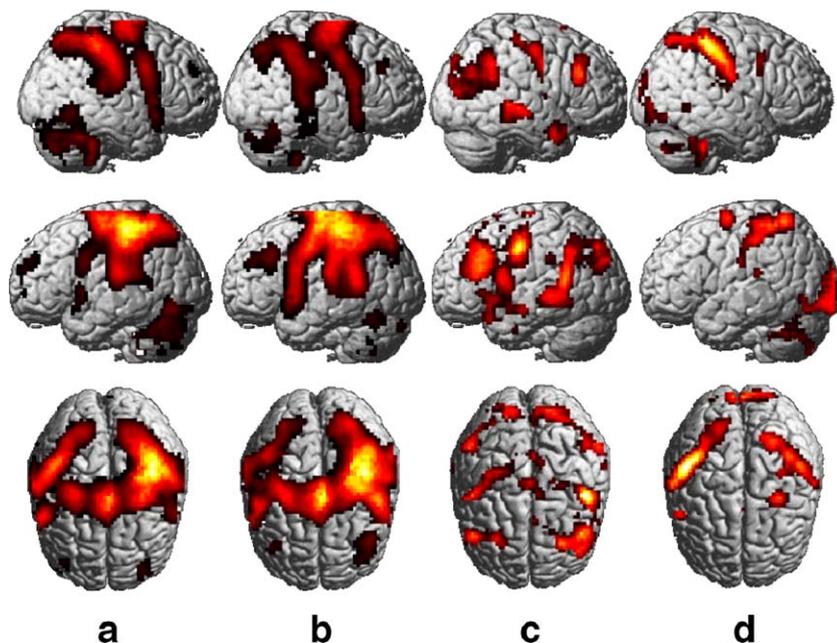

Fig. 3. fMRI group activation during the motion-related task (mT). Different views of a rendering of the SPM maps onto a standard single subject anatomical brain template. (a) Non-musician group (contrasted vs. rest); (b) musician group; (c) activations of the musician group (contrasted vs. non-musicians); (d) activations of the non-musician group (contrasted vs. musicians). SPMs FWE-corrected at cluster-level and thresholded at $P = 0.0001$ (a, b) and $P = 0.00005$ (c, d).

Pianists > Nonmusicians

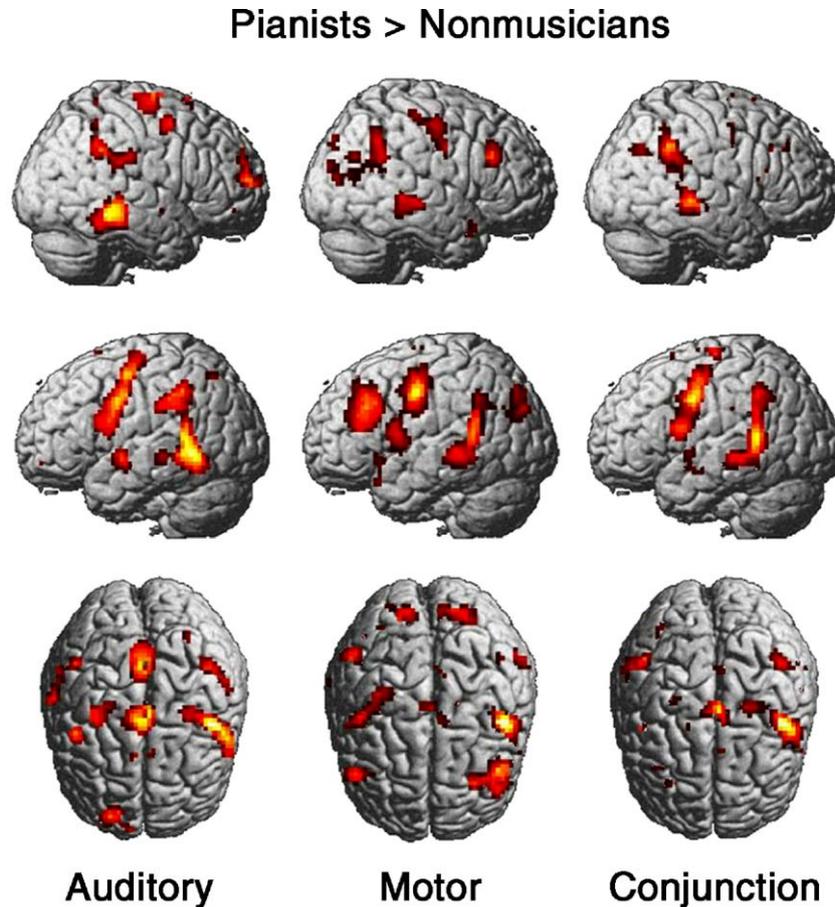

Auditory   **Motor**   **Conjunction**

Fig. 4. fMRI group differences summary and conjunction. Different views of a rendering of the SPM maps onto a standard single subject anatomical brain template. Every contrast is a group contrast pianists > non-musicians during the respective task. Left: acoustic task, middle: motion-related task, right: conjunction. SPMs thresholded below $P < 0.001$ (FWE-corrected) at cluster-level for $T = 5.36$ (aT), $T = 7.6$ (mT with extent threshold 10 voxels), and $T = 5.57$ (conjunction).

network was active in the pianist group, comprising the posterior STG, the precentral gyrus, and a part of the inferior frontal cortex (overlapping Broca's area).

Interestingly, the connected strip of activation extending from left digital M1 throughout the premotor areas in the lateral frontal lobe, ending in the left frontal operculum (BA 4-6/9-44), was found not only in the group comparison but also in every single pianist's activation contrast consistently (in six out of the seven cases, extending even to the temporal pole osculation). This strip displays activity in both the acoustic task and the motion-related task and hence is present in the conjunction as well. The same is true for another strip of activation, which extends from the left supramarginal gyrus into the left superior and middle temporal gyrus (BA 40-41/42-21/22). In the non-musicians, temporal lobe activations but not frontal or parietal activations were consistent on between-subject inspection. Especially a rudimentary strip of activation comparable to the frontal strip described in the pianists is only observed in two of the non-musicians.

Discussion

The professional pianists in the present study exhibited a greater activity in the network of areas outlined in Results.

Activation of motor areas

As for the activity in supplementary and premotor areas, one might compare the increased activity in the musicians in this study with the decreased activity in musicians (vs. non-musicians) during motor tasks found by other researchers (Jäncke et al., 2000; Krings et al., 2000). The reason for the decreased signal in those studies can be ascribed to the relatively high complexity of the motor tasks in those studies, which naturally led to a higher premotor and supplementary motor activity in the lesser skilled group, i.e., the non-musicians. The motion-related tasks of the present study, however, are much less demanding, thus the effect of recruiting more cortical resources in the musicians, was most probably due to the fact that the context of the mT was clearly music related for them (piano keyboard).

Lateralization and expert performance

The stronger prevalence of parts of the activated network in one hemisphere may be accounted for by methodological phenomena: the movement behavior in this experiment is limited to the right hand, thereby possibly creating an overall higher activation level in the left hemisphere. Furthermore, the influence of language-related processing like covert note naming in the pianists cannot be ruled out, however, all the participating pianists reported after the

Table 1
Active brain areas with significantly higher activation in pianists compared to non-musicians

	Lobe	Location	BA	Talairach coordinates			mm-GM
				x	y	z	
Acoustic task							
Right	Temporal	Middle temporal gyrus	BA 21	62	−35	−8	5
	Frontal	Superior frontal gyrus (SMA)	BA 6	6	−5	67	1
			BA 10	24	56	8	5
Left	Temporal	Middle temporal gyrus	BA 21	−48	−32	−1	3
		STG (Wernicke's area)	BA 22	−56	−3	−5	3
	Frontal	Precentral gyrus	BA 6	−45	−6	5	3
				−53	2	33	1
		Broca's area	BA 44	−50	7	13	5
	Parietal	Inferior parietal lobule	BA 40	−42	−42	38	1
				−53	−30	32	3
Motion-related task							
Right	Temporal	Middle temporal gyrus	BA 21	65	−32	−3	1
		Hippocampus		33	−24	−9	1
	Frontal	Precentral gyrus	BA 4/6	36	−15	42	5
				48	−9	47	1
		Medial frontal gyrus (SMA)	BA 6	3	−15	56	1
		Dorsolateral prefrontal gyrus	BA 46	53	28	26	5
	Parietal	Supramarginal gyrus	BA 40	48	−48	30	9
	Cortico/Limbic	Cingulate gyrus	BA 31	12	−12	45	1
			BA 23	6	−16	31	1
Left	Temporal	STG (Wernicke's area)	BA 22	−56	−46	13	1
	Frontal	Broca's area	BA 44	−50	6	11	7
		Dorsolateral prefrontal gyrus	BA 46	−45	25	32	3
		Precentral gyrus	BA 6	−50	−4	39	3
	Cortico/Limbic	Parahippocampal gyrus	BA 30	−15	−49	5	1
Conjunction							
Right	Temporal	Middle/Superior temporal gyrus	BA 21/22	65	−32	−3	1
	Parietal	Supramarginal gyrus	BA 40	48	−45	33	7
Left	Temporal	Middle/Superior temporal gyrus	BA 21/22	−53	−46	11	1
		(including Wernicke's area)		−56	−41	0	5
				−48	−32	−1	3
	Frontal	Precentral gyrus (SMA, PMA)	BA 6/44	−48	−3	50	3
		(including Broca's area)		−50	−1	36	1
				−50	7	13	5
	Parietal	Supramarginal gyrus	BA 40	−42	−45	33	3

experiment not to have used any verbal mental representation during the tasks. The left prevalence in the professionals may also be accounted for by different levels of expertise: Hickok et al. (2003) for instance, found the left middle temporal gyrus to be more active for speech tasks, but the right middle temporal gyrus to be more active for music tasks. We find a music effect in the respective region on the left side; however, whereas the former study dealt with non-musicians, the present study shows musician vs. non-musician contrasts, i.e., long-term training and skill effects. Maybe the simplified notion popular in the 70 s and 80 s that music processing is generally lateralized to the right in non-musicians, but 'switches' to the left in the course of becoming a professional musician (Bever and Chiarello, 1974; Altenmüller, 1986, 1989, also supported by Fabbro et al., 1990), still has some truth to it. Our data show, for example, that although both groups use both temporal lobes for melody perception in the aT (Figs. 2a, b), the between-group contrasts reveal a right-temporal prevalence in the non-musicians (Figs. 2c, d). Based on our findings, the most reasonable view is that lateralization effects are mostly study-specific, that means that areas of the putative network on both

hemispheres can be engaged in music tasks, but the extent of this activation (and which hemisphere prevails) will largely depend on additional parameters like skill level, task modality, task complexity, etc.

Specificity for music?

MIDI monitoring of the keypress sequences during mT indicated that the musicians motor patterns tended to be "melodically sequenced", whereas the non-musicians patterns were rather "motorically sequenced" (because they could not have any pitch representation of the silent motor patterns). Although this observation in the data is difficult to validate by quantitative measures, it introduces a possible overt performance difference between groups. The mT seems music-related to musicians and not music-related to non-musicians (a non-musical control task was not conducted). But this should not lead to the conclusion that the active network in the musicians is in any way specific to music processing. It is plausible to assume that the coactivation in the pianists does not reflect a general audiomotor integration system

specific to musicians nor a *music-specific* integration system acquired by music training. It is more likely that the phenomenon is based on *task-specificity*. It may be general in the sense that virtually every arbitrary auditory-motor coupling can be practiced over many years and lead to coactivation phenomena, but may be specific in the sense that the integration system only works in the trained sensory context.

Imagery

MIDI and EMG monitoring alone of course cannot eliminate the possibility that active motor imagery occurred during listening. In fact, the participating musicians did report some sort of imagery or mental sensation of sound during mT and of motor imagery during aT, however, as the instructions did not require any of this, the subjects also reported that these mental sensations were triggered automatically and that they 'could not help it' regardless of whether or not they attended to the task. It should be repeated here that the paradigm aimed at automatic processes but not necessarily pre-attentive processes. The cortical activation patterns and the subjects' self-reported sensations show considerable resemblance to active imagery, yet the subjects reported 'passive sensations' only, in the sense that they did not deliberately or voluntarily create these mental images. Imagery and automaticity are not mutually exclusive here but rather complementary.

A shared core network?

Our results demonstrate, besides musician-specific activations during passive listening and during silent finger movement, a network of areas active during both tasks. The character of the dissociation paradigm makes it reasonable to classify the active areas into modality-specific and domain-specific areas. Areas active during one of the conditions (aT or mT) but not the other – and therefore not visible in the conjunction – are considered modality-specific. Correspondingly, those areas that appear in the conjunction are considered auditory-motor coactive, integrative and thus specific to whatever the aT and mT have in common—which is: for a pianist, both tasks are related to piano playing. The major components of this putative network are the inferior frontal cortex/posterior frontal operculum, middle temporal gyrus, the posterior superior temporal gyrus, and the supramarginal gyrus. All of these areas are prominent on the left hemisphere.

Resent research on musicians and on music processing and performance has repeatedly revealed these very areas to be involved in a striking variety of musical tasks: motor preparation and execution (Lotze et al., 2003; Meister et al., 2004), imagery (Lotze et al., 2003; Meister et al., 2004), music perception (Ohnishi et al., 2001; Kölsch et al., 2002; Gaab et al., 2003; Levitin and Menon, 2003), and instrumental mirror systems (Hasegawa et al., 2004, Haslinger et al., 2005). We have deliberately pooled the aforementioned very different studies covering a whole variety of facets of music perception and production, and checked for the most frequent activation foci. Regardless of whether a music study paradigm involves perception or rather execution, the ensemble of main components correspond to what the current data show in the conjunction analysis, and appear to be crucial contributors to musician's skills—possibly a 'core network' of auditory-motor integration in musicians.

These components appear to be arranged in the two strips of activation as outlined in the results section, namely a temporo-frontal-to-central (BA 4-6/9-44), and a temporal-to-parietal strip (BA 40-41/42-21/22). From the background of language processing, it seems tempting to label the former "Broca-strip" or "action-strip", and the latter "Wernicke-strip" or "perception-strip" of musical audiomotor integration, although putatively equating these structures to functional cortical areas for speech processing may be misleading and does not receive immediate experimental support from the data presented here. The parallel, however, might be found in the observation that recent speech research shifts from the classical notion of a perception–production dissociation towards a joint representation (Price et al., 1996; Aboitiz and Garcia, 1997; Watkins and Paus, 2004; Watkins et al., 2003). The question arises why Broca and Wernicke's areas, though traditionally language-related, would be part of the cortical network dedicated to musical expression in skilled instrumentalists. The literature (see above) indicates a substantial role of these areas in music, just as in language. The importance of Broca's area for musicians has recently been shown not only functionally, but even structurally (Sluming et al., 2002).

Mirror systems in music

A bottom-up approach towards the clarification of the general functional relevance of Broca's area comes from the study of mirror neurons in monkeys (Rizzolatti and Fadiga, 1998). The idea of a cortical mirror system that codes action has recently been expanded from visual action observation to audiovisual and purely auditory domain (Kohler et al., 2002; Keysers et al., 2003; Romanski and Goldman-Rakic, 2002). In terms of cytoarchitecture, area F5 in the monkey resembles human BA 44 (Petrides and Pandya, 1999, 2002; Romanski et al., 1999). In fact, the 'mirror' functionality of area F5 has led researchers to consider this region the monkey's precursor of Broca's area (Rizzolatti and Arbib, 1998).

Three studies in musicians point towards a musical mirror system, one using auditory (Ohnishi et al., 2001), the second using visual (Hasegawa et al., 2004), and the third using auditory and visual action-observation (Haslinger et al., 2005). Especially the *inferior* portions of the fronto-parieto-temporal activation might, as Haslinger et al. (2005) have speculated, reflect the operation of a 'mirrormatching' system. Although our experiment, in contrast to Haslinger's et al. (2005), employs only passive *listening without accompanying visual observation* of piano movements, the distribution of activations in both studies looks strikingly similar. The audiovisual network may therefore be an audiomotor network at the same time.

What makes the auditory mirror system hypothesis particularly interesting is that the classic notion of Broca's area being dedicated to language and speech processing is now being expanded to cover a broad range of stimuli—including music.

Conclusions

The present study applies a passive task paradigm established in a previous study to a cross-sectional comparison of musicians and non-musicians utilizing fMRI.

The conjunction approach revealed a left-hemispheric supra-modal network being active in musicians but not non-musicians, comprising frontal, temporal, and parietal areas, regardless of task type and modality. This finding corroborates a broad range of

research on musicians and on music processing, and supports the idea that compartment of the cortex classically associated with language production may be involved in more general types of sensorimotor processing. The network recruited by professional musicians for listening to music as well as for performing musical actions may have properties of a transmodal mirror system.

Acknowledgments

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